

# COMPARATIVE FUNCTIONAL MORPHOLOGY OF CILIA OF *CORBICULA* (BIVALVIA: CORBICULIDAE): POSSIBLE CRITERIA FOR EFFECTOR AND PUTATIVE SENSORY TYPES

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## ABSTRACT

An outstanding feature of the behavior repertoire of *Corbicula fluminea* (Muller) considered here is the extreme mobility and responsiveness (especially to tactile stimuli) of the siphons. Lips of the anal siphon are notably the most responsive of the siphonal structures. Prolonged microscopic studies of serial sections of the clam's siphonal tissues revealed elaborate innervation of both siphons, but no indication of any sensory apparatus which could in turn be implicated in the distinctive behavior of the siphons. SEM studies of the epithelial surface of the anal siphon did reveal the presence of distinct, widely separated clusters of 12-20, short, upright cilia, which were seen to penetrate the "pebbled" nonmicrovillar epithelial surface. Distinctive structure of the ciliary clusters on the anal siphonal surface is especially evident when compared with SEM of other kinds of cilia in *Corbicula* (e.g. from gill, gut, mantle, gonoduct surface). These findings, along with behavioral evidence, indicate that the newly-discovered, peculiar siphonal ciliary tufts may well be the sensory organelles associated with the highly-developed tactile sensitivity of the anal siphon in *Corbicula*.

Von Uexkull (1934) characterized the *Umwelt*, the "world" relevant to an animal, as being comprised of both a sensory mode and an effector mode. With regard to the vast ciliation of many bivalved mollusks there is fairly sophisticated understanding of certain functions of effector cilia (Atkins, 1937a,b,c.; Purchon, 1956, 1978). Sensory function for ciliated or for any bivalved mollusk tissue is more difficult to establish. Accordingly, recent pertinent work on molluscan sensors is reviewed below. As is true for many non-vertebrate species (to paraphrase a comment on nematodes by Meglitsch, 1972, p. 242), we have little understanding of the sensory world bivalved mollusks inhabit. Unless the bivalve belongs to a species with well-differentiated sensors (for example, the eyes of *Pecten*), attribution of sensory function is often claimed on the basis of limited histological evidence, rarely accompanied by experimental evidence (Kraemer, 1969).

Examination of recent work on molluscan sensors reveals few investigators attempting to relate the organism's behavior to specific structures and functions of the animal. Of these, most work was done on delimited aspects of gastropod sensors. Work on chemical sense organs of opisthobranch snails has been done by Edlinger (1980). Photoreceptors of *Hermissenda crassicornis* are the subject of continuing research (e.g. Takeda, 1982). Statocysts of pulmonate gastropods have been the focus of study by Kovalev

et al. (1981). Buccal mechanoreceptors in the opisthobranch, *Navanax inermis* has been subjected to neurological study by Spray et al. (1980). Kovalev (1979) has studied response of the statocysts of *Helix vulgaris*; and Zaitseva et al. (1978) have examined structure-function relationships in the statocyst of *Lymnaea stagnalis*. Osphradial response in *L. stagnalis* has been the subject of a recent study by Kamardin (1976). Behavioral responses and their physiological bases are the focus of studies by Willows (1980) on *Tritonia diomedea*. Purely behavioral responses of the intertidal gastropod *Onchidium verruculatum* are examined by McFarlane (1980).

For bivalves, the recent literature is much more skimpy. Stephens (1978) studied escape responses in the queen scallop *Chlamys opercularis*. Prior et al. (1979) performed a behavioral and physiological study of "evasive" behavior in *Spisula solidissima*. Pichon et al. (1978) investigated the physiology of the sensory organ in the cruciform muscle of *Donax trunculus*. Raptorial siphonal apparatus and relation to feeding behavior and digestion in *Cardiomya planetica* is reported by Reid and Crosby (1980). Organization of certain freshwater bivalve osphradia and of statocysts was detailed by Kraemer (1978, 1981).

A continuing puzzle, much in need of investigation with modern techniques, is the fact that many bivalves respond to light although they have no "eyes" (e.g. Welsh, 1933; Bullock and Horridge, 1965; Kraemer, 1970). Some

years ago Kennedy (1960) provided a clue when he was able to demonstrate that the pallial nerve of *Spisula* sp. is responsive to certain light intensities. Bivalves are also frequently sensitive to water currents and tactile stimuli (Pavlov, 1885; Wenrich, 1916; Kraemer, 1970). Still, both environmental stimuli relevant to the animals and the physical means of detection employed by bivalves for these stimuli are scarcely understood, though statocysts have been implicated (Franc, 1960).

A few characteristics of *Corbicula fluminea* (Muller), subject of the present study, may appropriately be reviewed here. In contrast to indigenous freshwater bivalves with their flared mantles open to river currents, *C. fluminea* has a thickened, fused mantle, a narrowed pedal gape, a deep siphonal pocket and two muscular, extensible, highly mobile siphons (Fig. 1) with characteristic disposition of papillae (Kraemer, 1977, 1979; Britton and Morton, 1979). While behavioral observations do not seem to implicate light as a stimulus modality for *C. fluminea*, the slightest tactile stimulus, sudden water current change or jarring of the substratum all elicit siphonal response, especially of the conspicuous, characteristically peach-colored excurrent siphon. The response may involve movement of the papillae, the distal lip of the siphon, or the entire siphon. The full response typically involves contraction and then withdrawal of the whole siphon down into the siphonal pocket.

The present study is part of a continuing effort to understand certain characteristics of the behavior of *C. fluminea* in terms of its functional morphology. Ciliary organelles recently found on the mobile, behaviorally sensitive excurrent siphon are described below. Aspects of the functional morphology of essentially effector cilia on gills, palps and gonopore lips are compared and contrasted with the siphonal cilia. It will be argued that size, complexity and spacing of ciliary types in *C. fluminea* may well provide clues to their effector or sensory functions. For example, converging evi-

dence presented below from comparative histological and scanning electron microscopic studies and behavioral observations is adduced to argue for probable sensory status for the siphonal ciliary organelles.

## MATERIALS AND METHODS

Histological serial sections of *C. fluminea*, made as described elsewhere (Kraemer and Lott, 1977), were used to examine ciliation and innervation of siphons, labial palps and gills and to check observations of moving cilia on living tissues, and on scanning electron micrographs. Prolonged observations were made before and during the present study on responsiveness of the siphons, especially the excurrent siphon, to tactile stimuli. Lengthy observations were similarly made on the mode of movement of several kinds of cilia on the gills and labial palps of fresh tissues with a Wild M5 stereomicroscope and with a Leitz Ortholux microscope equipped for bright-field transmitted light.

Living specimens used in this study were obtained from intake bays at Arkansas Nuclear One, near Lake Dardanelle on the Arkansas River at Russellville, Arkansas in the fall of 1981 and the spring of 1982. Subsequently the animals were relaxed in Nembutal solution. Siphonal tissues as well as tissues from gills, labial palps and gonopore region were removed, fixed in 2.0% gluteraldehyde, and then moved through cold phosphate buffer solutions and a dehydration series of ethanols. The tissues were next critical-point dried using liquid CO<sub>2</sub>, mounted on stubs with silver adhesive solution and coated with 15 nm of gold, using a Polaron SEM Coating Unit, E 500. The samples were viewed with an ISI-60 Scanning Electron Microscope (SEM) at 30 Kv and a working distance of 15 nm.

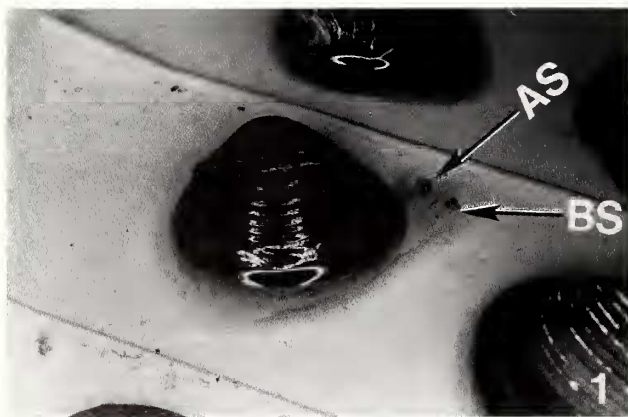


Fig. 1. Living specimen of *Corbicula fluminea* (Muller), with siphons extended. AS, excurrent siphon; BS, incurrent siphon. Horizontal field width = 12 cm.

## RESULTS

### Excurrent siphon epithelium

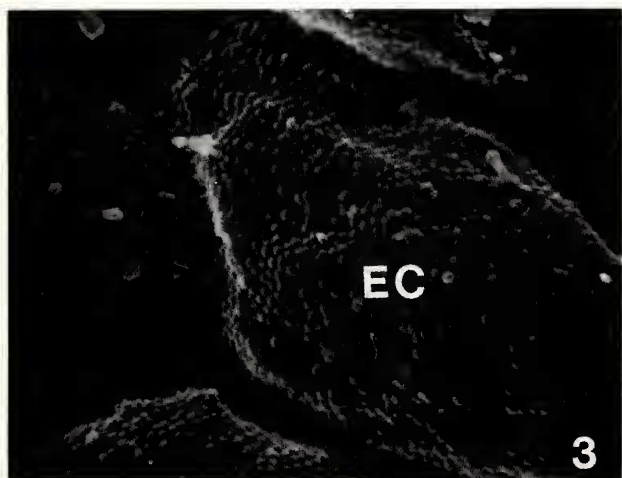
In examining the surface of the excurrent siphon with SEM, the characteristic distribution of siphonal papillae (Britton and Morton, 1979) is clearly evident (Fig. 2). One can see a few cilia on the (contracted) surface of the distal tips of a number of the papillae. A closer look at the siphonal epithelial cells' surface shows a "pebbled," probably non-microvillar surface (Fig. 3). In addition, at widely dispersed intervals (8–10  $\mu\text{m}$  apart), discrete clusters of cilia protrude through the epithelial cell surface. Each cluster is composed of 16 to 20, curved, short (2–2.5  $\mu\text{m}$  "tall") cilia (Fig. 4 a,b). These isolated ciliary clusters have a very different aspect, size and structure from all cilia examined on other epithelial cell surfaces of *C. fluminea*.



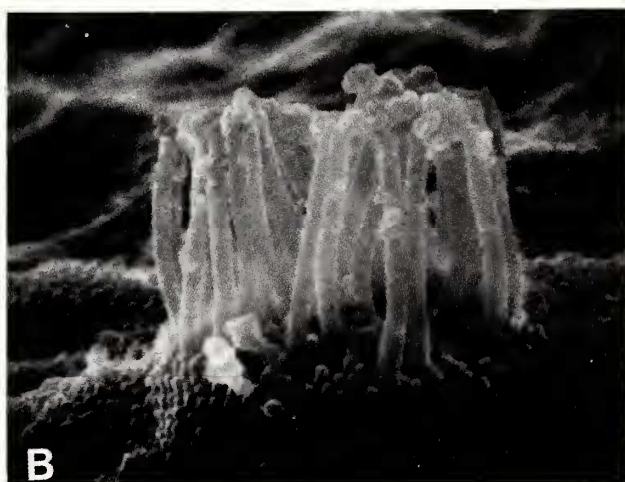
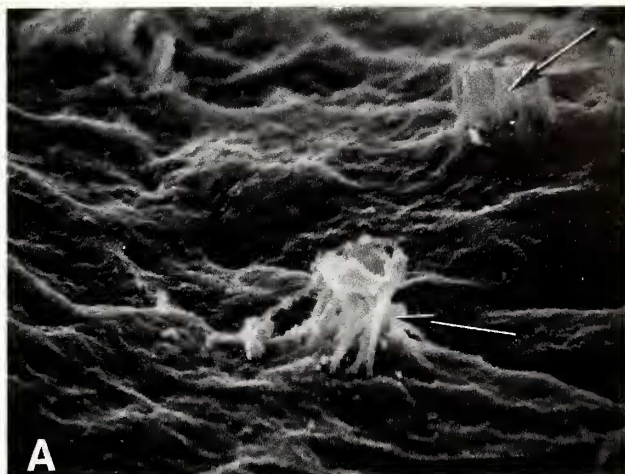
**Fig. 2.** Low power, SEM of the excurrent (upper) and incurrent (lower) siphons of *Corbicula fluminea* (Muller). Arrow indicates the smooth, non-papillated inner lip of the excurrent siphon, where putative sensory ciliary organelles have been found. Small slender cilia were noted on the (contracted) tips of some of the papillae of the excurrent siphon, also. Horizontal field width = 3 mm.

### Labial palps

In living tissues examined for this study, the labial cilia were observed to move food particles toward the mouth in a

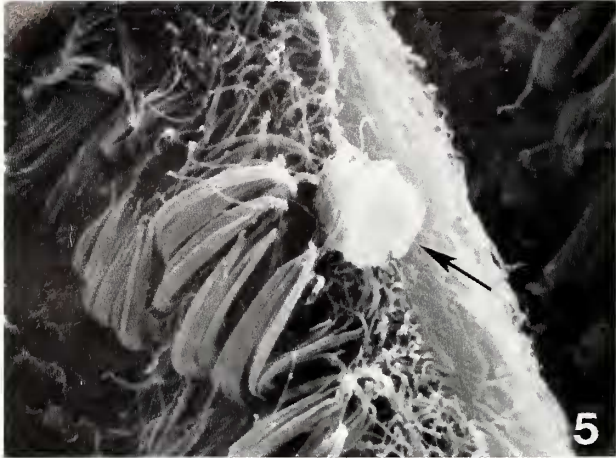


**Fig. 3.** SEM of distal surface of parts of several excurrent siphonal epithelial cells. EC, distal surface of an epithelial cell. Horizontal field width = 7  $\mu\text{m}$ .



**Fig. 4.** SEM showing widely spaced ciliary clumps on surface of excurrent siphonal epithelium. (A) arrows indicate ciliary clumps. Horizontal field width = 20  $\mu\text{m}$ , (B) a single ciliary clump protruding through the surface of an epithelial cell. Horizontal field width = 8  $\mu\text{m}$ .

long zig-zag. That is, particles could be followed as they were moved to the right along one ciliary row and then to the left along the succeeding ciliary row. Food particles were also observed to be moved in a direct, row-to-row course over the inner surface of the palps and into the mouth. Seen with SEM, the labial cilia were large (10–12  $\mu\text{m}$  long). SEM evidence for both kinds of palp ciliary movement described above was found. Direction of movement of a particle along a ciliary row (during zig-zag movement) was clearly evident with SEM when particles were photographed lodged within ciliary rows. In such instances cilia were almost invariably seen pushed together on one side ("behind") but not on the



**Fig. 5.** SEM of labial palp cilia in *Corbicula fluminea*. Cilia are long and dense. Note crowding of cilia under particle (arrow) where effective ciliary "force" is apparently being applied. Horizontal field width = 30  $\mu\text{m}$ .

other side ("in front") of the moving particle. The manner of "boosting" a food particle from one ciliary row to another is indicated in Fig. 5, where the distal tips of a group of large labial cilia may be seen tilted together "under" a food particle.

### External surface of gill

With SEM, the distal edges of the gills near the food grooves were seen to display a landscape crowded with long, slender cilia (Fig. 6). Lateral surfaces of the gills, even with light microscopy, manifested certain slender cilia in addition to the large stiff cilia lining the outer edges of the water tubes



**Fig. 6.** SEM of ciliary surface of outer gill of *Corbicula fluminea*. Edges of several gill laminae are shown and location of food groove is indicated (arrow). Horizontal field width = 150  $\mu\text{m}$ .

(Fig. 7a). With SEM three different kinds of cilia were clearly seen organized in dense, alternating rows (Fig. 7 b,c). Most striking were the large double banks of multiple cilia (or cirri) that resemble those described by Owen and McCrae (1976) on *Nucula sulcata*. These were clearly distinguishable from the more slender, single cilia of the neighboring rows (Fig. 7 d,e). The several types of cilia on the gill surfaces were observed with light microscopy in living tissues to be associated with different kinds and directions of particle sorting and movement.

With SEM it appeared that: (a) the large, double-rowed, paddle-shaped, multiple cilia (cirri) with their elaborate rootlets were apparently responsible for the major movements of particles vertically along the gill lamellae; (b) the large, single-rowed multiple cilia would seem to function in selective sorting of particles; and (c) the long, slender cilia logically appeared to be those that move particles over the surface of the gill and toward currents generated by the paddle-shaped cilia.

### Surface of gonoduct

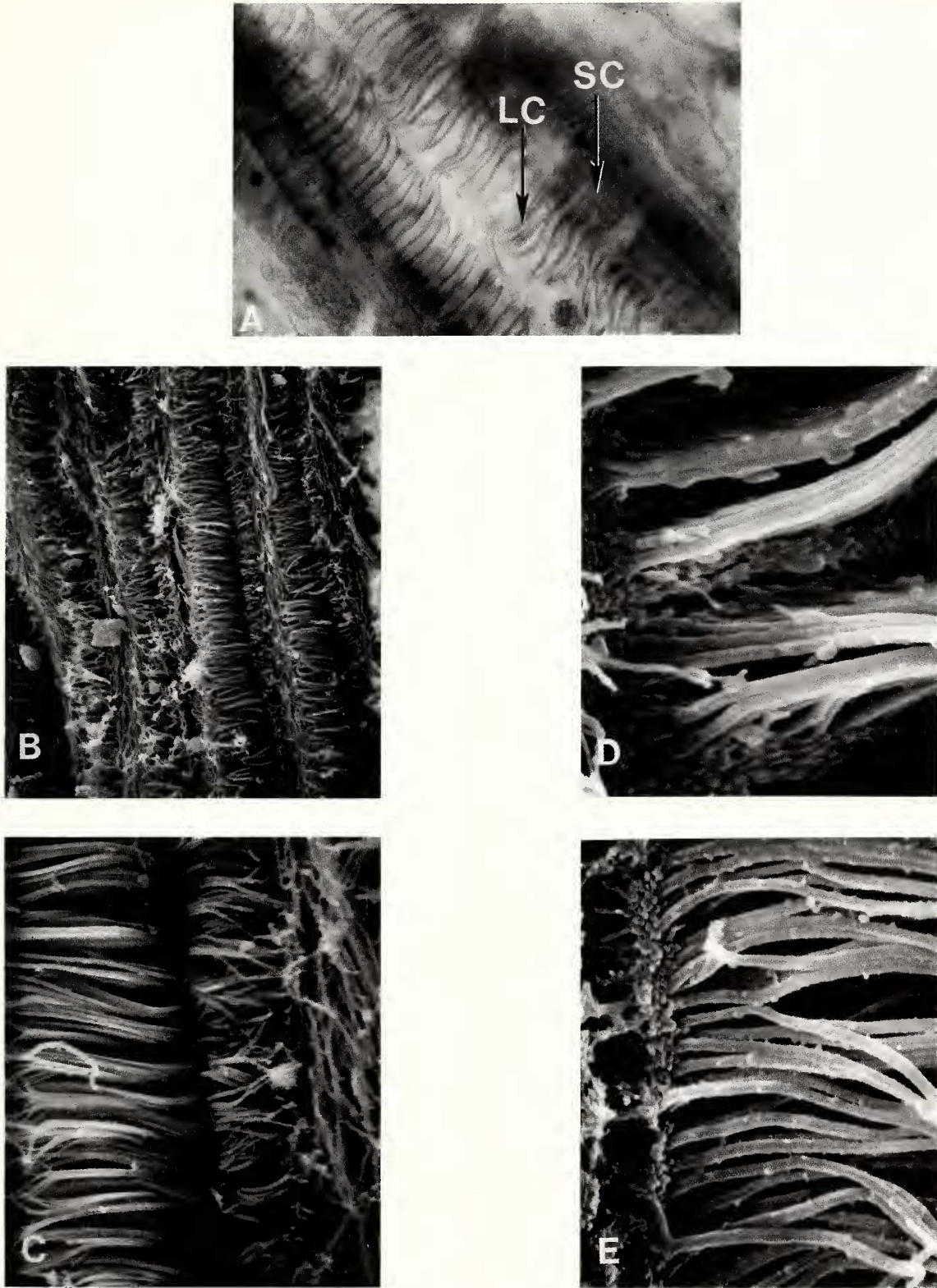
While the large cilia on the surface of the gonoduct (gonopore lips) were readily seen with light microscopy, their patchy distribution was revealed only with SEM. With SEM the gonoduct surface was seen to be covered with round patches (about 10  $\mu\text{m}$  in diameter) of long (10–12  $\mu\text{m}$  long) cilia (Fig. 8). Functional rationale for the gonoduct surface cilia and their distinctive distribution is unclear.

### Interior surface of gill

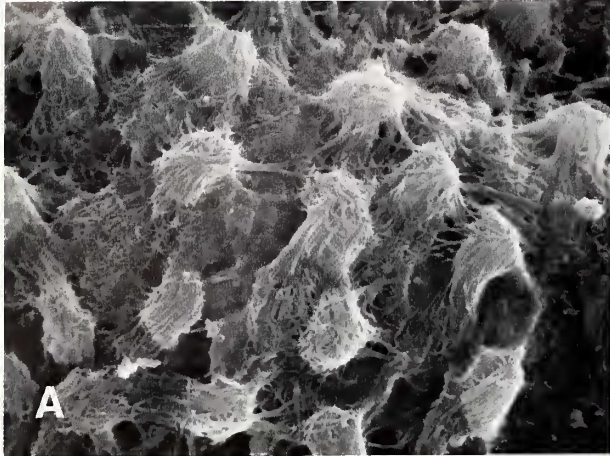
The only gill cilia found in *C. fluminea* in this study that resemble in size and shape the small cilia of the siphonal surface described above, were found at rare intervals within the cavities of the gravid inner gill (Fig. 9). These were single small cilia with unknown function. They may be associated with transport of embryos within the inner gill cavities.

## SUMMARY AND DISCUSSION

With the help of SEM, it has been possible in this study to characterize several types of cilia in *C. fluminea* not previously observed. Light microscopic observations of moving cilia on living tissues of labial palps helped to establish the direction of movement of food particles over their surface; and SEM made it possible to note the manner in which groups of effector cilia provide the force to move particles. Light microscopic observations of both serial histological sections and of living tissues of gill made it evident that some cilia were larger than others, and were involved in moving particles in different ways. SEM made it possible to determine that at least three kinds of effector gill cilia are involved, respectively, in producing several specific kinds of particle movement.



**Fig. 7.** Lateral gill surface ciliation of *Corbicula fluminea*. **(A)** light micrograph. LC, large cilia, SC, smaller cilia. Horizontal field width = 2 mm. **(B)** SEM showing alternating rows of three kinds of cilia. Horizontal field width = 130  $\mu\text{m}$ . **(C)** Detail of B. Large double cilia are at left. Horizontal field width = 30  $\mu\text{m}$ . **(D)** Large double cilia are seen to be double rows of multiple cilia (cirri). Horizontal field width = 6  $\mu\text{m}$ . **(E)** Large single cilia. Horizontal field width = 7  $\mu\text{m}$ .



**Fig. 8.** Ciliation of external gonopore lip surface in *Corbicula fluminea*. **(A)** SEM of large ciliary clumps distributed over the surface of the gonopore lip. Horizontal field width  $65\ \mu\text{m}$ . **(B)** Detail of A. Cilia are large and interlaced with cilia from neighboring clumps. Horizontal field width =  $6\ \mu\text{m}$ .

Light microscopic observations of gonoduct serial sections examined in connection with this study, revealed apparent groups of long cilia on the lips of the gonopore. SEM confirmed that the cilia are indeed clumped, and exhibit a patterned arrangement of patches of large, complex cilia on the epithelial surface. Function of these cilia has not been determined; but their large size, complexity and location indicate that they may function as effectors in moving ova or embryos that exit from the gonoducts.

Responsiveness of the siphons, especially the distal lip of the excurrent siphon of *C. fluminea*, to tactile stimuli was repeatedly observed throughout the study. Light microscopic studies of siphonal serial sections during this work revealed extensive innervation of siphonal musculature and the distal edges of the siphons. No histological evidence of siphonal



**Fig. 9.** SEM of interior surface of inner, gravid gill of *Corbicula fluminea*. Widely spaced, small single cilia of unknown function (arrows). Horizontal field width =  $20\ \mu\text{m}$ .

sensory structures was found; and no conspicuous cilia were noted on the siphonal surface. With SEM in this study, an apparently "new" organelle was seen in the form of widely separated clusters of very small, curved cilia on the surface of epithelial cells of the distal lip of the responsive, excurrent siphon.

Because of their location on an exquisitely sensitive, highly innervated surface and because of their small size and distinctive appearance, it seems likely that the siphonal ciliary clumps are suitable candidates for sensory organelles. The siphonal ciliary clusters present a striking contrast when compared with cilia that have demonstrable effector functions, such as the large, complex and closely crowded cilia of the labial palps and the gill surfaces. The siphonal ciliary clumps are more nearly similar to scanty, slender cilia of unknown function found during this study in the interior of the gill cavities.

How are sensory functions for inconspicuous organelles of bivalve mollusks to be determined? One searches the literature in vain for research on bivalve sensors that in any way matches the work of Atkins (1937a,b,c), Stasek (1965), Jorgensen (1966, 1974) or Purchon (1978) on effector cilia. Using essentially morphological criteria Stasek (1966) characterized a small "ciliary sense organ" associated with the pallial eye of *Tridacna maxima*, and Kraemer (1981) did as much for the osphradial complex of two freshwater bivalves (*Lampsilis ventricosa* and *Corbicula fluminea*). Of course, physiological evidence is needed; but present day physiological techniques seem scarcely equal to the task. What alternatives are there, in the absence of physiological evidence? In the present study, the siphonal ciliary organelles described above could have been overlooked if the author had not been acutely aware of siphonal sensitivity of *C. fluminea*. The present work at least seems to indicate that per-

sistent observation of the whole animal's behavior, and of the context and movements of living parts of the animal (e.g. cilia) may assist in evaluating functional morphology from histological and ultrastructural evidence.

From this study it may be suggested that further work on bivalve cilia may provide more evidence to indicate: (1) bivalves possess a heretofore unsuspected variety of ciliary types, each evidently suited to particular functions; (2) effector cilia types will typically be found to be large, complex and bunched in big groups, while sensory cilia will typically be found to be smaller, fewer, more isolated; and (3) cues to function of the morphological cilia types may continually be sought in careful ongoing observations of the behavior of the living organisms.

### ACKNOWLEDGMENTS

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